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STUDIES OF LOCALIZED STAGES OF GROWTH IN SOME COMMON NEW ENGLAND PLANTS.

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In the following are given some of the stages in detail found in a few of our common plants, and some general notes which may be safely drawn, and which may be useful in studying plants from this point of view. The cases given are not chosen as particularly striking ones, but are such as would come naturally under the notice of any one. In a following paper the writer hopes to present more striking examples from some of the less generally known plants now in the Botanic Gardens of Harvard University. The few given, however, will show the truth of the principle involved as well as more striking ones.

In a paper by Robert T. Jackson, "Localized Stages in Development of Plants and Animals," *Memoirs Boston Society of Natural History*, Vol. V, No. 4, 1899, this principle was worked out and applied to plants. It was there applied to shoots and various growths of trees almost exclusively. It is in the spirit of that paper that I have attempted this one, giving the results of my study of plants from this point of view. My thanks are due to Dr. Jackson for reading this in manuscript and for many suggestions.

The new point intended to be brought out here is the application of the principle of localized stages to the early spring growth of herbaceous plants. These are adult plants, not young plants or seedlings. The principle is also applied to the stages immediately preceding the flower.

The principle of localized stages in development, to quote from the above paper, is that, "throughout the life of the individual, stages may be found in localized parts, which are similar to stages found in the young and the equivalent of which are to be sought in the adults of ancestral groups." This principle may be well demonstrated in a greater or less completeness in each of the following examples.

Viola pedata L. (Bird's-Foot Violet).

Under this species Gray's *Manual* gives, "leaves all 3–5-divided, or at the earliest only parted, the lateral divisions 2–3-parted, all linear or narrowly spatulate, sometimes 2–3-toothed or cut at the apex," thus recognizing the fact of the differences in the leaves but with no significance of the various forms or connection between them.

On April 18, 1902, a study was made of the leaves of this species in adult plants which were then well started. Among the larger and stronger plants it was found that the earliest leaves went back in the accompanying series usually to Pl. I, Figs. 10 or 11. After further search plants were found with the leaves on the outside of the rosette, similar to Figs. 9, 8, or 7. Noticing that the smaller plants seemed to be simpler or more primitive, attention was turned to them, and some small ones were found with the outside leaves going back to Fig. 6, and the smallest to Figs. 5 or 4. These were along a woods road in a somewhat dry, sandy place. In the middle of this road, where there was very little vegetation, were found plants evidently very young and weak, with the result that some were obtained with the simple leaves shown in Figs. 3, 2, and 1. That these were not seedlings was shown by the rootstock. They were probably weak plants of the preceding year.

In nearly all the stages shown many specimens were obtained of each stage, and in all cases enough to warrant the form as not abnormal. Where the outer leaves were most primitive the more complete were the stages before the typical leaves were produced in the center. Seedlings of this plant were not obtained, but the earliest of the stages given are very similar to corresponding ones of *Viola tricolor* L. in both young and adult. Later stages would naturally be specific. The seedling would probably not repeat all of the stages given here, but the majority of them. The data here being fairly complete will be referred to again later.

Chelidonium majus L. (Celandine).

Seedlings of this plant were found at Arlington Heights in May, among the adult plants, and afforded a very convenient opportunity to study the relations of the two.

The leaves of the seedling after the cotyledons are developed as follows (Pl. II, Figs. 1, 2): First leaf usually slightly trilobed and trinerved; second leaf usually decidedly five-lobed and five-nerved; the third leaf is decidedly trilobed, with the median lobe notched, lateral ones entire or with one notch. From the third on, the trilobed character persists for a short period, the leaves becoming, later, three-pinnate, five-pinnate, and so on.

In comparing this with the first leaves of the adult plant when it starts from the ground in the spring, a striking likeness is at once noted. In the plant shown in Pl. II, Fig. 3, the first leaf is exactly comparable to the second leaf of the seedling, and the second to the third of the seedling. The third leaf is like the three-parted one of the seedling, the fourth similar. The fifth is five-pinnate, and so on. In all cases where the first formed leaves were found on the plant, these comparisons were found to be true. It was especially noticeable in the plants found at Arlington Heights, which were on a sloping gravel bank with poorer nourishment than in other cases noticed in Cambridge. In this plant the early development in spring growth representing localized stages, and in the seedling representing direct development, not only show great similarity but may be exactly compared stage by stage.

Aquilegia canadensis L. (Wild Columbine).

The seedlings of this plant have the first nepionic leaves typically trifoliolate, with the terminal leaflet having two well-marked notches and each of the lateral leaflets one less-marked notch on the lower side. By raising a number of the seedlings of this plant there was found a marked variation from the typical form. In two cases the first nepionic leaves were trifoliolate, but both the terminal and lateral leaflets were entire, no sign of notches being present. The second leaves in the two cases given were typical of the first of the other seedlings, thus showing that these two individuals were less accelerated in development than the others. These two repeated the character of a trifoliolate leaf with entire edges, which is usually dropped out in the development of the seedling.

By comparison with the early spring growth of adult plants, the first leaves of some weaker individuals were trifoliolate and entire, as are those of the two seedlings noted above. This is, then, not an accidental variation, but a true stage, which in the seedling is usually skipped by acceleration of development, and rarely appears there. In several cases the first leaves were like the typical first leaves of the seedling. This, then, shows two rates of acceleration, as it takes one longer to arrive at a certain stage than it does another.

A striking similarity is noticed in the leaves immediately preceding the flower. At the base of the flower stalk the leaves are normal, but higher up the number of leaflets is reduced until, a short distance below the flower, there appears a trifoliolate leaf with notches varying considerably, some being like the typical first nepionic leaf of the seedling, others variously notched. The majority, however, are like the seedling. The next leaf above usually drops out the notches and has an entire outline. This can be directly compared to the earlier stage noted in two seedlings and in the average simple leaves of spring growth of the adult plant. Just beneath the flower is often found a single leaf, entire and exactly comparable to the terminal leaflet of the trifoliolate leaf. Thus at the flower the leaves retrace the steps which they went through in the early growth of the plant and in the reverse order. This last stage — the simple leaf below the flower — is more primitive than anything that is found in the seedling, showing that localized stages may be used to fill in the steps which are crowded out by the acceleration of development in the seedling.

Ranunculus acris L. (Buttercup).

This species has the typical leaves three-divided, and the divisions considerably cleft and toothed, but the seedling starts off with fairly simple nepionic leaves (Pl. II, Fig. 4). Comparing the localized stages shown in the early spring growth with the direct development of the seedling, a great similarity is again noted. The plants were well started when observed, and weak growths had to be largely depended upon to show the stages. Pl. II, Fig. 5, shows a leaf of which one-half is comparable to the first nepionic leaf of the seedling. The other half is like the second nepionic. Here, then, is a leaf showing an acceleration of development in its two halves, — the half with two lobes being more accelerated than the other. This is often noted in compound leaves which are pinnate, — there being fewer leaflets on one side than on the other, — but is less often definitely shown in simple leaves. A first leaf of spring growth is figured, Pl. II, Fig. 6, which is comparable to the second nepionic leaf. The steps in complication of the lobes and nervation are shown in Figs. 7–9, and the seedling in its later development passes through similar stages.

Beneath the flower the leaves become more simple usually by four distinctly reverse, but often varied, steps. The lower one of the four has about the same number of divisions as Fig. 8, but is drawn out into linear divisions. Higher up is a leaf that may be compared to the second nepionic of the seedling, or to the leaf figured in localized development (Fig. 5), in that it has five lobes. It is, like the preceding, deeply cut and elongated. Above this is a three-lobed leaf of the same character and in its lobing comparable to the first nepionic leaf of the seedling. Just beneath the flower is usually a simple, elongated leaf, showing once more a localized stage in the adult plant more primitive than any of the stages shown in the direct development of the seedling.

This species is one which is usually well developed in the early spring, and these earlier and weaker forms are hard to find without careful searching. The first formed leaves quickly dry, curl, and then drop off.

Spiræa salicifolia L. (Common Meadowsweet).

This is not herbaceous, and the stem, unlike the others before noted, is woody, and the early spring growth is from the buds at the sides as well as new shoots from the ground. Such a lateral growth is figured, Pl. III, Fig. 3. The first leaf indications are mere bracts. The first of what may be called the true leaves is entire, lanceolate, with a simple median vein. This is the first in the series and the simplest. This seems to be a case like that noted under *Aquilegia canadensis*, where a stage is found simpler than that of the ordinary seedling first stage, as the first nepionic leaves of two species of Spiræa as figured by Lubbock are like No. 2 of Fig. 3. The second leaf is cuneate and tridentate, trinerved, the broadest part near the tip. The third leaf is five-dentate like the second nepionic leaf figured by Lubbock. The complexity of dentations increases and the broadest portion of the leaf moves from near the tip to near the base. The leaves become doubly serrate, but the tip holds the form of the second leaf given, throughout.

The spire formed by the flowers usually has one or more of the lower branches with more leaves than flowers, and here the reversal of the stages is well shown. Near the main stalk the leaves are typical, but moving distally along the branch they will be seen to lose little by little in the number of dentations. This keeps on until there are but three, as in the second leaf figured, and then there are several simple ones. The wedge shape, with its broadest part toward the tip, is not reassumed, but in dentations the stages are exactly reversed beneath the flowers.

Tanacetum vulgare L. (Tansy).

As far as was found, the seedling of this species has not been published, and therefore it is given in a little more detail than the others (Pl. III, Figs. 4 and 5).

Cotyledons glabrous, subfleshy; lamina oblong, obtuse, sessile. The first nepionic leaves are paired and vary considerably. As a whole they are spatulate, obtuse, and may be distally toothed. Ten seedlings in a single pot were compared as to their first nepionic leaves as follows:

Both first leaves simple	2
One simple, one one-notched	1
One simple, one two-notched	1
Both one-notched	2
One one-notched, one two-notched	1
Both two-notched	3
	10

This crude table is enough to show the individual variation of seedlings under the laws of acceleration of development and the consequent necessity of making sure of the typical stages.

The second pair of nepionic leaves have typically two lateral teeth on each side in some cases, with more complicated forms than this, but even in this case, so far as seen, only one of the pair has the more complicated form, the other being typical. The midrib begins to be distinct.

The next leaves are quite dissected and begin to decidedly resemble the typical adult leaf. It may have in the third pair of nepionic leaves from three to seven or more lateral teeth on each side, and these may also be divided or notched.

Among the adult plants at the very base in the first spring growth, leaves may be found which repeat many of the simpler conditions. Fig. 6 is decidedly three-parted, much as the first nepionic leaf in many ways, but less strikingly so than Fig. 7, which is quite like the second nepionic leaf of the seedling. Figs. 8 and 9 are like later seedling stages. All of these leaves are from the base of fresh spring growths.

The flowers of this plant are in a dense corymb, each portion of which comes from the axil of a leaf. The leaves in the upper part become inconspicuous, but repeat, however, many of the characters seen in the seedling and in the reverse order, those immediately below the upper heads being like the first and second nepionic leaves in the number of teeth and general character. This is exactly comparable to the principles of senescence of the late Professor Hyatt, stages occurring in the old age of the individual corresponding to stages passed through in nepionic development, but in the reverse order of succession. He has shown this at length in his "Genesis of the Arietidæ," published in part as a paper of the Museum of Comparative Zoölogy of Cambridge, and as No. 673 of the *Smithsonian Contributions*. It is given more simply and concisely in a paper, "Cycle in the Life of the Individual (Ontogeny) and in the Evolution of its Own Group (Phylogeny)," *Proceedings of the American Academy of Arts and Sciences*, Vol. XXXII, No. 10, as well as in other papers. This case seems to be comparable in that it is a failure to develop the full characters of an earlier adult condition, due to the strength of the plant going into the production of flower and seed instead of developing leaves. The tip of the leaf in all cases repeats the tridentate character of the first nepionic leaf, both in the tip of the leaf proper and in the tips of all the divisions.

Viola tricolor L. (Pansy).

This plant is very seldom a perennial, but often comes up from the rootstock the second year. Such plants are easily obtained, and so exactly do the stages compare with the seedling that were it not for the rootstock and the absence of cotyledons the two might be easily mixed. The seedling is figured by Lubbock, *Seedlings* (1892), and in that and in seedlings examined the stages were exceedingly like those of the early spring growth from a rootstock. The reversal of these stages beneath the flower is seen with varying definiteness. The old single form known as heart's-ease seems to show this best. The number of notches decreases and the leaves return to the forms seen in the beginning, those directly beneath the flower being exactly like the first of the spring growth of the adult and the first nepionic (Pl. III, Figs. 1 and 2).

Rosa rubiginosa L. (Sweet Brier).

In this plant, perhaps, of those given here, the stages are most easily and completely seen. The seedling varies, having the first nepionic leaf single as in Pl. IV, Fig. 1, or it may be trifoliolate like the second leaf of Fig. 1, as in Fig. 2; in each case the second nepionic leaf is trifoliolate, as well as several following ones. Then the number of leaflets increases to five, and in the full-grown plant becomes seven. In the first spring growth the first leaf, especially upon the lower or weaker parts of the plant, is very often trifoliolate, like the second nepionic leaf in all cases and like the first in some. In some cases, however, a simple leaf may be found, but rarely. When it does appear, it may be compared to the simple leaf seen in the first nepionic leaf of Fig. 1. After this trifoliolate leaf in the spring growth of the adult is one of five leaflets, then usually five leaflets until the flowering stage. Then the number drops by the same steps that it increases, but in the reverse order. Going toward the flower, leaves are encountered with five, then three leaflets, until finally just below the flower there is a simple one. Here, then, are repeated the exact steps by actual count of the stages of the seedling in the early spring growth, and as exact a reversal of the same stages beneath the flower. The same is true of *Rosa lucida* and other species (Pl. IV, Fig. 3).

Although these examples given might be multiplied almost without number, they will do to illustrate several general principles which may be drawn from them. The various conditions are more or less combined in any actual case, as they often are in such problems, but the effect of each may be noted nevertheless.

First, the relation between the occurrence of the earliest stages and the age of the plant. The plant coming up the second year, other conditions being the same, seems to be more primitive in its first characters than older and stronger plants. It therefore repeats more stages in arriving at the typical form than older individuals. The case of *Viola pedata* illustrated this, the young plants of the preceding year being the ones in which the earliest stages were noticed. In some plants, however, the typical leaf of the species is not reached for several years. The young trees of *Carya alba* Nutt., the shagbark hickory, have when very young — the second year, for example — only single and trifoliolate leaves, and it is some time before the number rises to five leaflets. The typical one of seven leaflets does not appear until quite a late period.

Weak individuals are more apt to show earlier stages than are more vigorous plants. They represent plants which are less accelerated in their development, not attaining the characters usual in plants of their age and other conditions. This is true whether the whole is weak or whether the growth comes from adventitious or weaker buds. The same is true of plants injured by outside agencies; for example, when the leaves are stripped by insects and a later growth put out from the weaker buds, before undeveloped.

Soil and moisture conditions come into play here. The poor sandy soil and lack of moisture mentioned in the first two examples given, shows its effect by producing weak individuals. Plants in poor, dry soil often repeat stages not seen in strong, vigorous plants in other places.

In studying these localized stages, especially in the early spring growth of herbaceous plants, some things must be especially looked out for. The first leaves which appear are often very small and would be overlooked unless they were being sought for especially. Many of these plants which start very early in the spring adopt the rosette form, and these first early leaves are hidden under the later ones. These small early leaves are usually delicate and soon wither and drop off, especially in rapid growth or where the rosette form is adopted. For these reasons many plants, even in early spring, may show no traces of the very early stages which they would have shown if examined a short time before. The surest way to find these first leaves is to notice where the plant is growing the year before and mark it in some way so that it may be looked for the following spring.

As shown, seedlings may vary considerably, and also these stages, so that to avoid errors there is necessary a knowledge of the seedling or allied ones, and of ancestral forms. By a close study of these localized stages and their variations — within limits — in many individuals, steps in the phylogeny may be determined which it would be impossible to fix in any other way. Many stages may be found in this way that in the acceleration of the seedling are crowded out of the record preserved there.

Coupled with a knowledge of the seedlings and of ancestral forms these localized stages may be used to great advantage in determining not only the phylogeny in a broad way, but the relations, especially to plants in the same genus or family. By comparing the character of the stages repeated and the acceleration with which they are gone through with, something may be learned of the position of the species in relation to others within the genus, according to the general principle that greater acceleration of development means a higher form. Comparison of seedlings of different species may also determine this to a considerable extent, but many seedlings of each species should be compared to get the relation of the variation. Thus from the seedlings of various species of Aquilegia raised and compared, a definite relation was noticed in regard to the relative difference in time of appearance of the same stage in different species. In this way localized stages, together with a comparative study of seedlings, may be made to yield profitable results in a field where there is otherwise very little data to depend on.

EXPLANATION OF PLATES.

Leaves are numbered in order of their development, except below the flower,— there, in the reverse order. c = cotyledons.

Figures drawn from nature by the writer.

PLATE I.

Viola pedata L.

FIG. 1. First leaf of spring growth of plant one year old. Found in middle of old woods road-dry soil. × 1½.

FIGS. 2, 3. Second and third leaves of same plant. × 1.

FIGS. 4, 5. First leaves of spring growth of plants found at side of same road in slightly more favorable conditions. Plants small and evidently weak. × 1.

FIG. 6. First leaf of slightly stronger plant in same place. × 1.

FIGS. 7–9. First leaves of decidedly stronger individuals in better situations. × 1.

FIGS. 10, 11. First leaves of thrifty plants of more than one year's growth. × 1.

FIGS. 12–14. Later leaves of same plants. × 1.

FIG. 15. Most complex leaf noted in strongest and best developed plant. × 1.

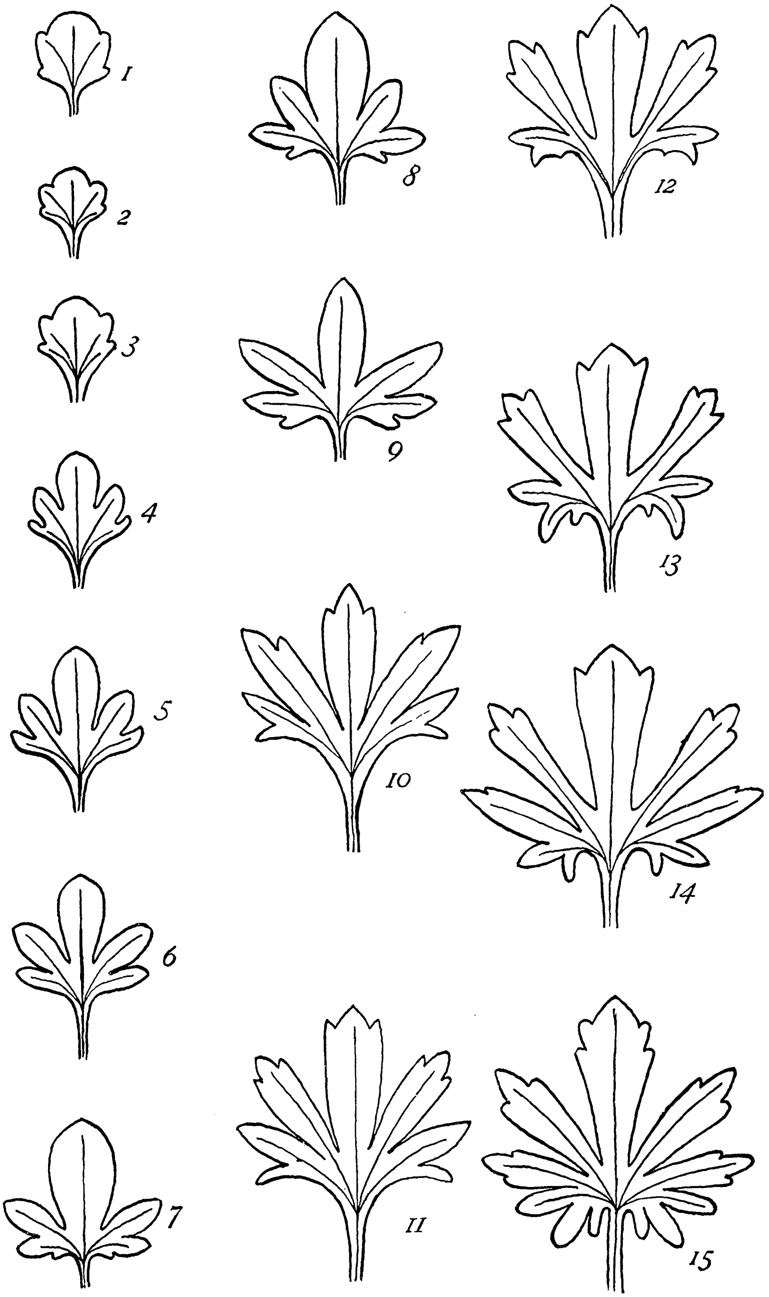

PLATE I.

PLATE II.

(All natural size.)

Chelidonium majus L.

FIG. 1. Seedling showing cotyledons and first and second nepionic leaves.

FIG. 2. Seedling as preceding, but showing also third nepionic leaf.

FIG. 3. Leaves of early spring growth. In sandy soil at Arlington Heights, Mass. 4th, 6th, and 8th leaves not shown — each like the one immediately preceding.

Ranunculus acris L.

FIG. 4. Seedling showing cotyledons and 1st, 2d, and 3d nepionic leaves.

FIG. 5. Simplest leaf found in an adult plant; first leaf of spring growth of weak plant. Two halves of leaf show difference in acceleration of development. Compare right half with 1 of Fig. 4; left half with 2 of same figure.

FIG. 6. First leaf of spring growth in weak plant. Compare with 2, Fig. 4.

FIG. 7. First spring growth of a weak shoot. Compare with 2, 3, Fig. 4.

FIGS. 8, 9. Later stages in adult plant and complication of the network of veins.

FIG. 10. Typical adult leaf.

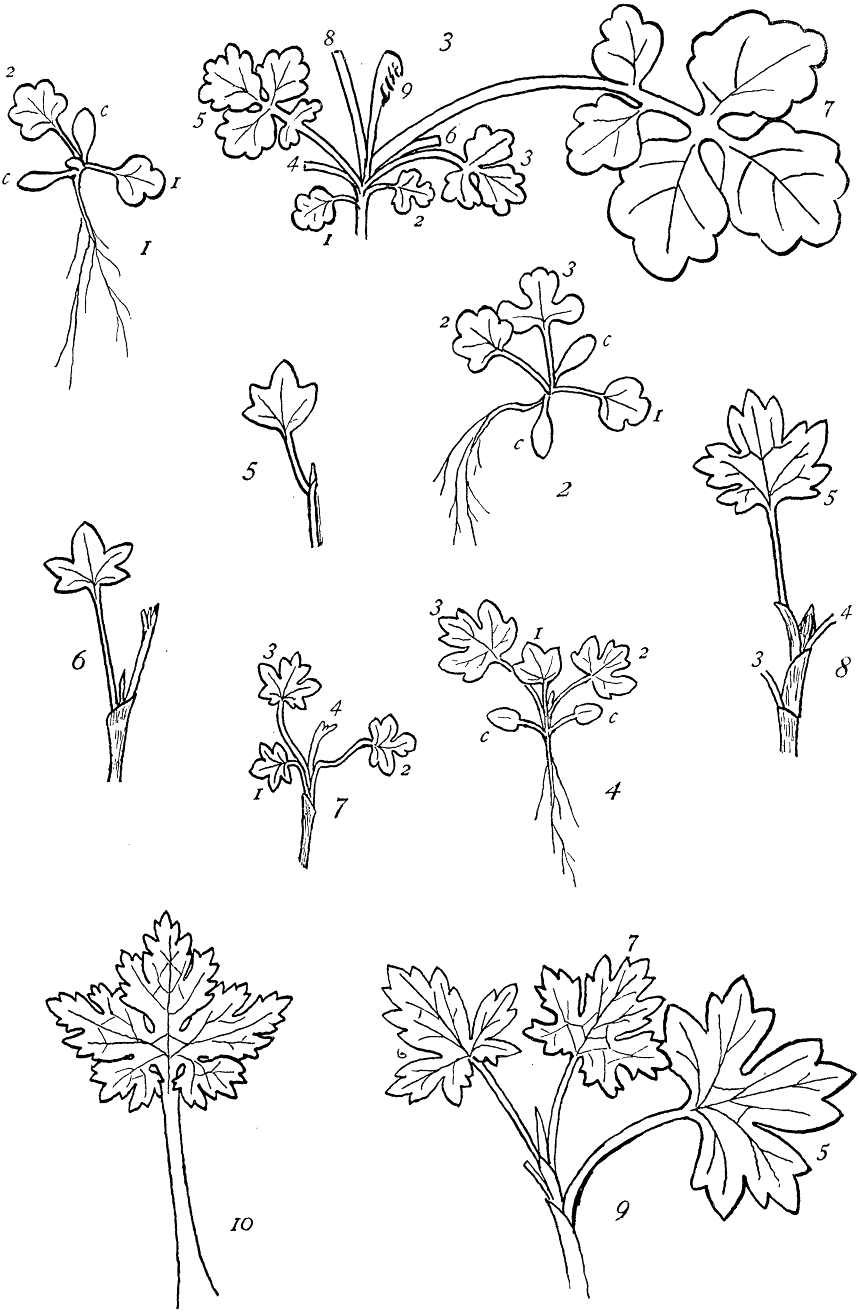

PLATE II.

PLATE III.

(All natural size.)

Viola tricolor L.

FIG. 1. Stages in early spring growth from rootstock of preceding year.

FIG. 2. Stages below flower. Numbered in reverse order of development for comparison with preceding.

Spiræa salicifolia L.

FIG. 3. Growth from lateral bud on plant of previous year. Bract-like leaves at base not numbered.

Tanacetum vulgare L.

FIG. 4. Seedling with cotyledons and typical pair of first nepionic leaves.

FIG. 5. Seedling with second pair of nepionic leaves also.

FIGS. 6–10. Leaves found near the base of adult plants in spring growth. Compare 6 and 7 with 1 and 2 of Figs. 4, 5.

FIG. 11. Simplest leaf to be found after early spring growth has withered. Very complex when compared with Figs. 6–9.

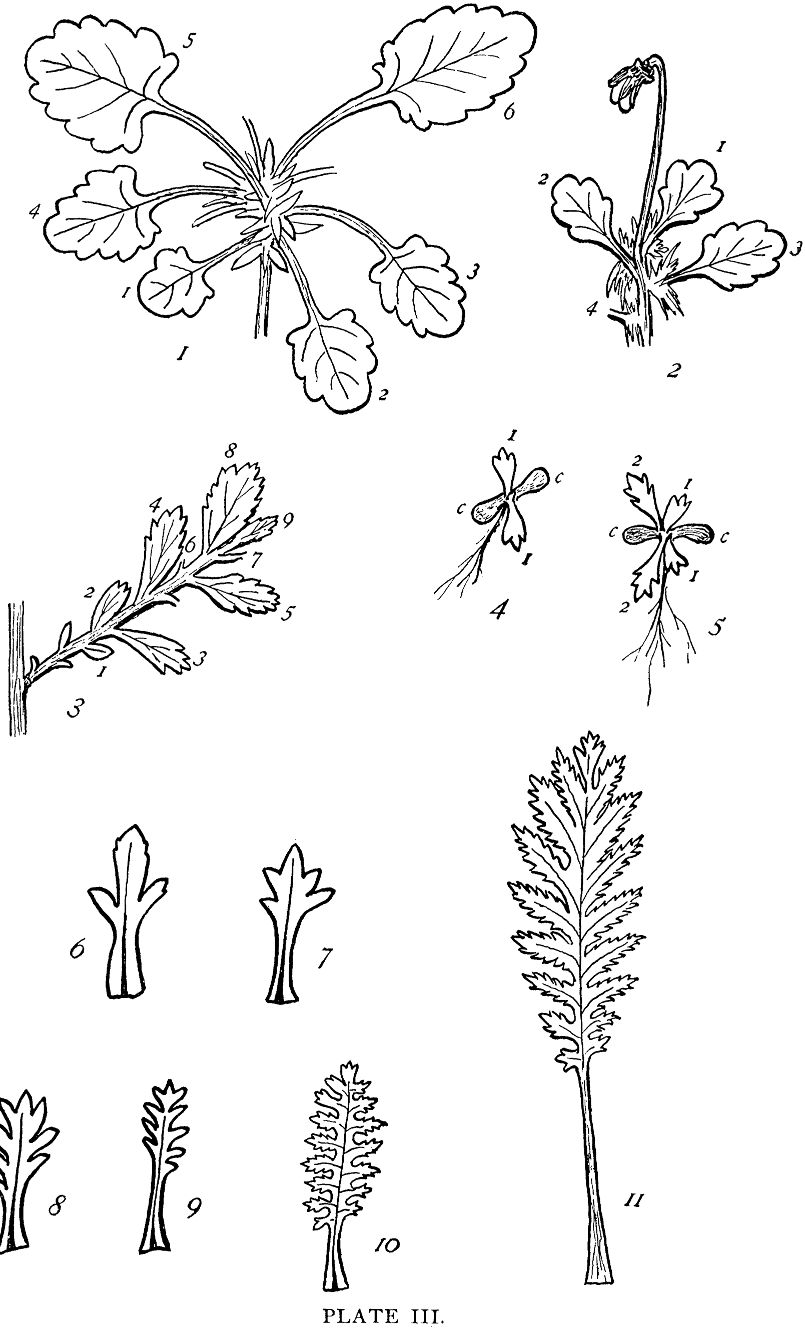

PLATE III.

PLATE IV.

(All natural size.)

Rosa rubiginosa L.

FIG. 1. Seedling showing cotyledons, and simple first and trifoliolate second nepionic leaves.

FIG. 2. Seedling with both first and second nepionic leaves trifoliolate.

Rosa lucida L.

FIG. 3. Stages from first leaf of spring growth, 1, to flowering stage, 12.

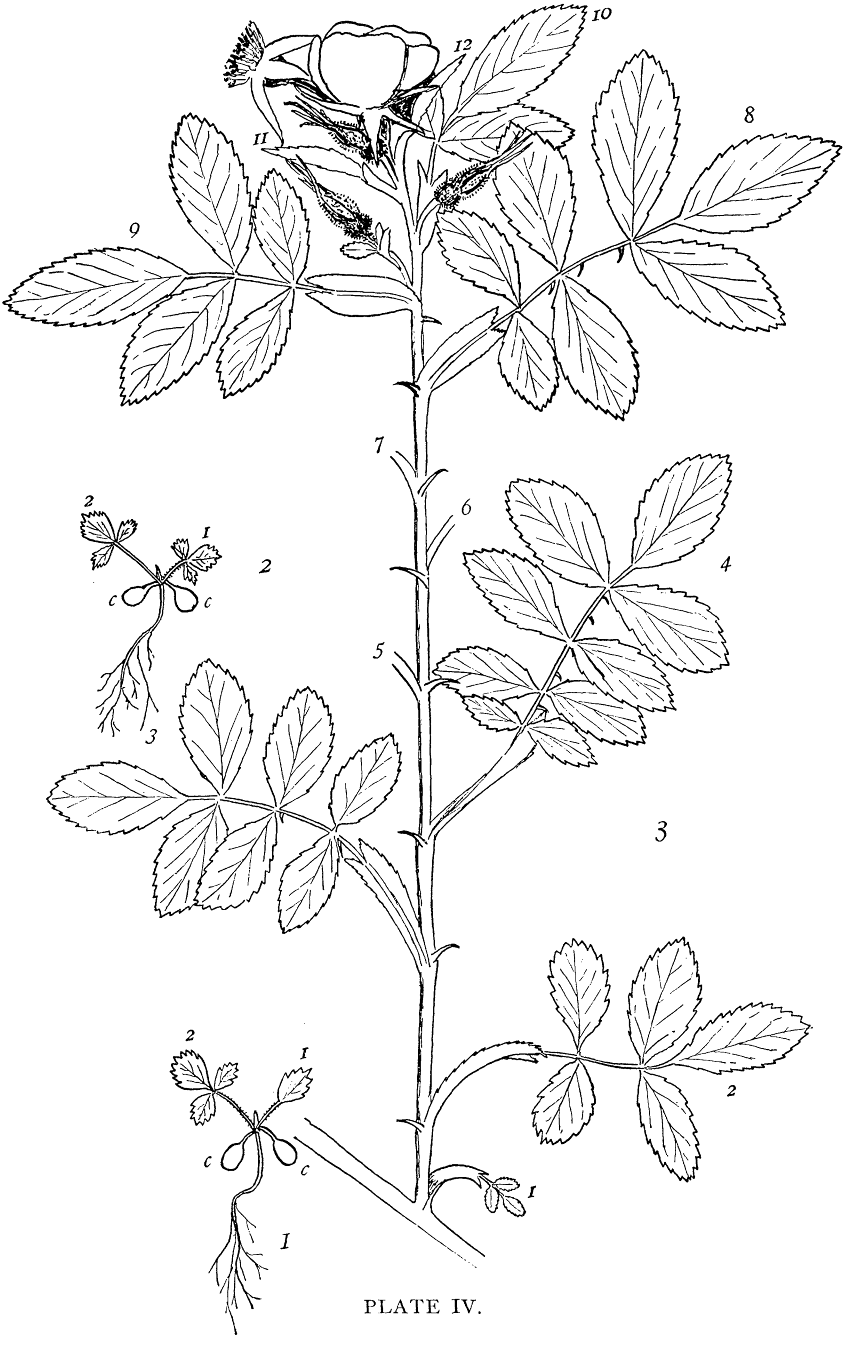

PLATE IV.

PLATE V.

Aquilegia canadensis L.

FIG. 1. Seedling with first nepionic leaf simple in outline, second normal. × 1.

FIG. 2. Seedling with normal form of first and second nepionic leaves. × 1.

FIG. 3. Stages in early spring growth from ground. Compare with seedlings and Fig. 4. × ½.

FIG. 4. Stages below flower, partly diagrammatic in apparent crowding, but each leaf in its relative position and shape. Numbered in reverse order for comparison with Fig. 3 and seedlings.

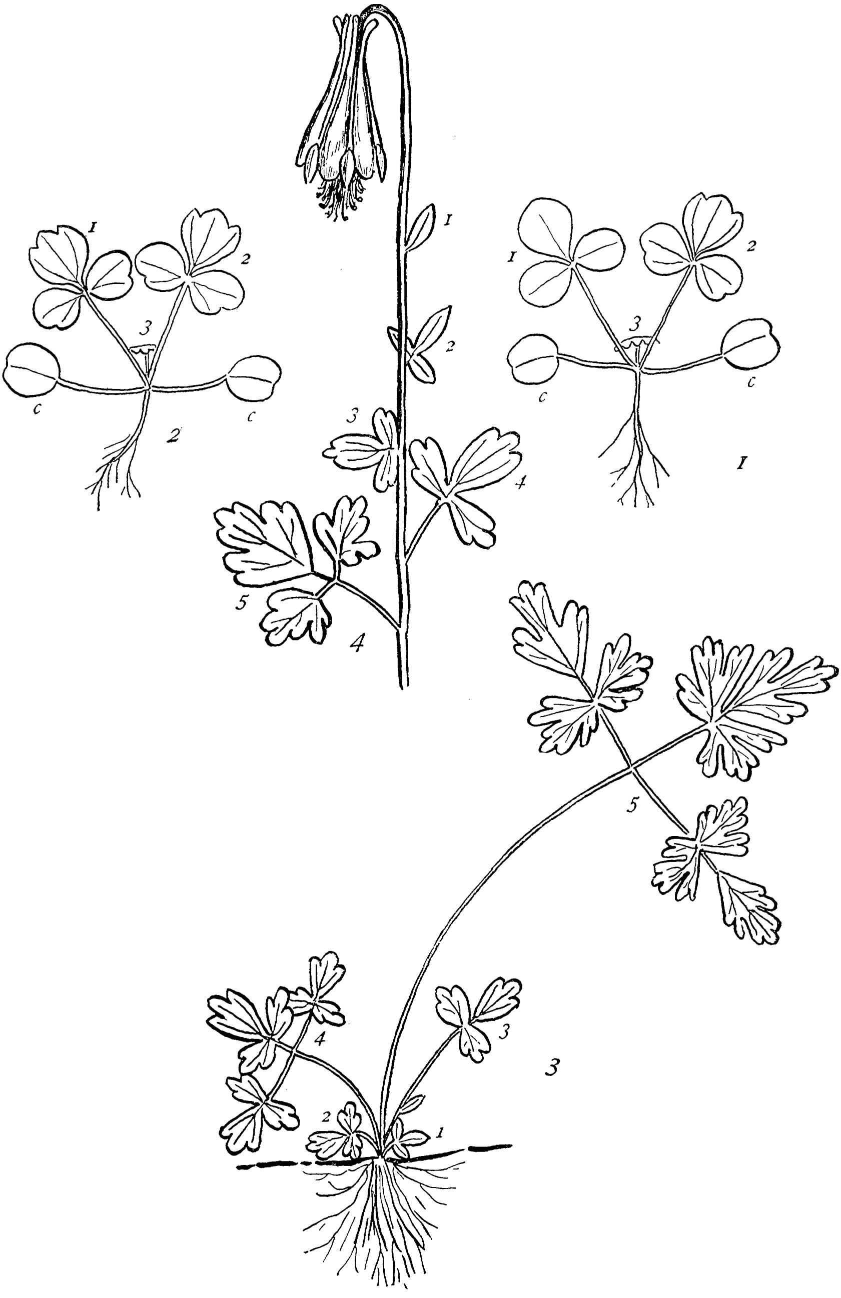

PLATE V.